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Versatility of carotenoids: An integrated view on diversity, evolution, functional roles and environmental interactions

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ABSTRACT

Carotenoids have traditionally been subscribed to their role as accessory pigments in photosynthesis. However, the large and growing body of literature investigated on the field have revealed that carotenoids fulfil a plethora of essential roles in plants but also in animals and in humans. Recent studies emphasizing the functional role of molecules derived from carotenoids oxidation as β-cyclocitral or dihydroactinidiolide led to a renewed interest, opening a new era for the carotenoids research. This review brings together the knowledge obtained so far regarding diversity and functions of carotenoids, highlighting carotenoids versatility and the remarkable parallel roles of carotenoids in both plants and in animals. Evolutionary aspects and the responses of carotenoids to biotic and abiotic stresses are discussed. Furthermore, we outline the way in which one can understand the environmental regulation to enhance carotenoid content in food. In addition, an up-to-date overview of carotenoids as elements of information storage system for the responses to environmental signals is provided together with suggestions for future directions of research.

1. Introduction

Looking through the window in autumn, one may realize that leaves are showing all their colourful attributes due to the carotenoids. These compounds become apparent in leaves of deciduous trees during autumn in temperate climates, when degradation of chlorophylls unmasks the yellow–orange colour of carotenoids. Though they seem to be hidden, carotenoids are one of the most widespread and ubiquitous lipid soluble pigments in nature (e.g. in leaves, fruits, flowers, teguments, etc.) and so far, more than 750 naturally occurring carotenoids have been identified (Britton et al., 2004). Carotenoids are produced by all photosynthetic organisms, by fungi and by non-photosynthetic bacteria and conversely, they are required in the diet of animals as antioxidants or vitamins, but also to produce their tissues pigmentation, as is the case of the feathers of birds or the exoskeleton of crustaceans. Only three arthropod species (red aphids, spider mites and gall midges) have obtained the enzymatic machinery for the carotenoids biosynthesis due to the genes lateral transfer from fungi (Moran and Jarvik, 2010; Grbić et al., 2011; Cobbs et al., 2013).

Chemically, carotenoids are tetraterpenes and their structures are based on 40-carbon polyene chain with conjugated double bonds (3–13) along this chain (Fig. 1). Remarkably, carotenoid compounds only differ in the following chemical characteristics, which give rise to the different carotenoids structures: (i) the presence and number of oxygen atoms in the molecule (oxygenated carotenoids are xanthophylls and non-oxygenated are carotenes), (ii) the hydrogenation of the carbon polyene chain, (ii) the cyclization at one/both ends of the molecule, usually with a ε-ionone or β-ionone rings and the (iv) length of the chromophore (Britton, 1995; Meléndez-Martínez et al., 2007). Carotenoids have electronic and spectroscopic properties (Christensen et al., 2004) and then depending on the configuration and length of the chromophore of conjugated double bonds, the UV/vis spectrum (and then the colour) changes (Meléndez-Martínez et al., 2007).

Abbreviations: ABA, abscisic acid; α-C, α-carotene; A, antheraxanthin; AM, arbuscular mycorrhizal; β-C, β-carotene; β-Cyc, β-cyclocitral; Dd, diadinoxanthin; Dd-Dt-cycle, xanthophyll cycle involving diadinoxanthin and diatoxanthin; Dt, diatoxanthin; GGDP, geranylgeranyl pyrophosphate; L, lutein; Lx, lutein epoxide; LxL-cycle, xanthophyll cycle involving lutein epoxide and lutein; N, neoxanthin; NPQ, non photochemical quenching; $^1O_2$, singlet oxygen; QTL, quantitative trait loci; ROS, reactive oxygen species; PSY, phytoene synthase; TAIR, The Arabidopsis Information Resource; V, violaxanthin; VAZ-cycle, xanthophyll cycle involving the carotenoids violaxanthin, antheraxanthin and zeaxanthin; Z, zeaxanthin.

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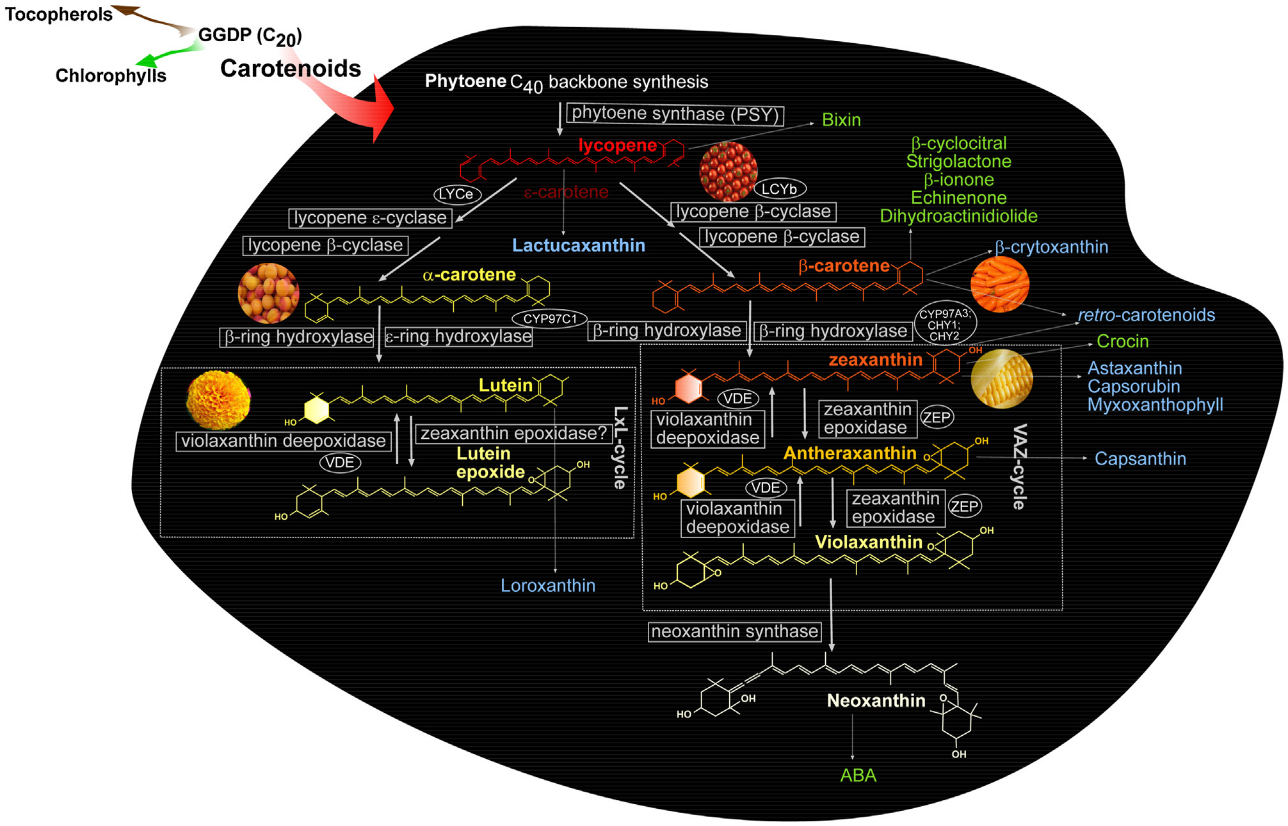

Fig. 1. Carotenoids, which are terpenoids, are synthesized from the molecule geranylgeranyl pyrophosphate (C_{20}), as chlorophylls and tocopherols, which are other terpenoid-derived compounds. The biochemical biosynthetic pathway starting point is the phytoene (C_{40}, colourless carotenoid) that give rise to the rest of the main carotenoids of photosynthetic tissues. Chemical structures of the main carotenoids in the pathway are drawn, showing their natural colours based on the UV/vis spectrum. Photographs of fruits/flower are shown as examples of the carotenoids abundance in those organs: tomatoes for the carotenoid lycopene, carrots for the carotenoid β-C, corn for the xanthophyll Z, apricots for the carotene α-C and marigold for the xanthophyll L. The xanthophylls participating in thermal energy dissipation through the operation of the VAZ- or LxL-cycle are shown inside the dashed squares. Note that the key structural differences in the end-rings between the xanthophylls L, Z and A are indicated with colour inside each of the rings. The enzymes and gene names (according to Table 1) are indicated in squares and circles, respectively. Molecules derived from carotenoids oxidation as β-cyclocitral, strigolactone, β-ionone, echinenone, dihydroactinidiolide, bixin, crocin and ABA are shown in green colour. The names of the compounds in blue colour are other "non-ubiquitous" carotenoids and unusual carotenoids. (For interpretation of the references to colour in this figure legend as well as in the text, the reader is referred to the web version of this article.)

This is illustrated in Fig. 1, where main carotenoids in plants are showing their natural colours, due to their absorbance spectra. As for example, β-carotene (β-C) is orange (with absorption maxima at 451 and 481 nm in the organic solvent acetone) or lutein (L) is yellow (with spectral maxima at 446 and 476 nm in acetone). Carotenoids function, which has been demonstrated to be essential for plants (explained in detailed in the forthcoming Section 4), is determined, therefore, by physical and chemical properties of these molecules (Britton, 2008). Indeed, carotenoids, contrasting with other plant pigments as anthocyanins or betalains, play essential, multiple and diverse roles in the photosynthetic activity of plants, as light harvesting compounds (Durchan et al., 2014), photoprotective molecules (Domonkos et al., 2013), or assembling elements in the photosynthetic apparatus (Havaux, 1998). They also fulfil important functions in the interactions plant–environment (Esteban et al., 2015), including the provision of essential intermediates for biosynthesis of plant phytohormones (Walter and Strack, 2011) or bioactive mediators (Bouvier et al., 2005), or as visual cues to attract pollinators and seed dispersers (Schaefer et al., 2004). In other organisms, carotenoids decorate the tegument of animals (Pérez-Rodríguez, 2009) or they are essential components of mammalian diets, as the precursors of vitamin A (von Lintig, 2012). Vitamin A deficiency caused by a diet poor in carotenoids is a global health problem (WHO, 2009). Then, carotenoids are likewise important for society and economy in areas as agriculture, livestock and human food; but also in health, cosmetic and pharmaceutical industry.

It is becoming increasingly difficult to ignore that carotenoids have become an intriguing research topic in the last decade, due to their versatility in both plants and animals (especially in humans). Together with these fundamental functions, some new roles have recently been described in plants, as chemical quenchers of singlet oxygen ($^1O_2$) and/or as signalling molecules (Ramel et al., 2012; Shumbe et al., 2014). In this review, therefore, we explore the diversity (Section 2) and functions of carotenoids, with special interest on new roles, while, highlighting interesting parallels between carotenoids function in plants and animals (Section 4). Evolutionary aspects are outlined (Section 3) and the responses of carotenoids to biotic and abiotic stress are depicted (Section 5). This review examines the approaches conducted until now to regulate the carotenoids pool in crops by environmental regulation (Section 6). Finally, we provide an up-to-date overview of carotenoids as elements of stress memory, and therefore, as information storage mechanism for the responses to signals in the plant–environment interactions (Section 7).

2. Carotenoids diversity in nature

Purpleness of purple bacteria, brownness of brown algae, yellowness of birds' feathers or orangeness of carrots are examples